RESEARCH ARTICLE

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Environmental influences on larval duration, growth and magnitude of settlement of a coral reef fish

Abstract The influence of environmental variables on the planktonic growth, pelagic larval duration and settlement magnitude was examined for the coral reef surgeonfish *Acanthurus chirurgus*. Newly settled fish were collected daily from patch reefs in the San Blas Archipelago, Caribbean Panama for 3.5 years. Environmental influences on growth were examined at three different life history stages: from 0 to 6 days, 7 to 25 days and from 26 to 50 days after hatching. Larval growth was correlated, using multiple regression techniques, with a combination of factors including solar radiation, rainfall, and along-shore winds. Depending on the life history stage, these accounted for 13–38% of the variation in growth rates when all the months were included in the analyses. Correlations between environmental variables and growth also varied among seasons and were stronger in the dry than in the wet season. During the dry season solar radiation, rainfall and along-shore winds described 57%, 86% and 74% of the variability in growth between 0 and 6 days, 7 and 25 days and 26 and 50 days, respectively. During the wet season rainfall, along-shore winds and temperature only described 38% of the variability in early growth and 27% of growth just before settlement. No significant model was found to describe growth 7–25 days after hatching during the wet season. Rainfall, solar radiation and along-shore winds were negatively correlated with growth up to 25 days after hatching but positively correlated as larvae approached settlement at a mean age of 52 days. Over 65% of the variability in pelagic larval duration was accounted for by a regression model that included solar radiation and along-shore winds. When data sets from wet and dry seasons were analysed separately, along-shore winds accounted for 67% of the change in larval duration in the dry season, and solar radiation accounted for 23% of the variation in larval duration in the wet season. Only 22% of the variability in settlement intensity could be described by solar radiation and temperature, when all months of the year were included in the analysis. Solar radiation and rainfall were included in a regression model that accounted for 40% of the variation in numbers of fish settling during the dry season. This study suggests that the levels of solar radiation, along-shore winds and rainfall during the early larval life can have important effects on the growth, larval duration and consequently, the settlement magnitude of marine fishes. Results also highlight the need to account for seasonality and ontogeny in studies of environmental influences.

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Introduction

Marine fish larvae suffer very high mortality (Hjort 1914; Bailey and Houde 1989; Doherty 1991), which may be strongly influenced by growth rates. Larvae that grow quickly are the first to attain the sizes necessary to become juveniles or enter juvenile habitats (Houde 1987). Consequently, fast growing fish are exposed to planktonic predators for a shorter period of time and may be less vulnerable to some predators than slow growing fish of the same cohort (Anderson 1988; Cushing 1990).

To date, most of the evidence supporting these concepts (collectively termed the "growth-mortality

hypothesis") originates from studies in temperate regions. However, recent work has also shown that in tropical reef fishes larval condition and/or growth are important determinants of survivorship in the planktonic (Bergenius et al. 2002; Wilson and Meekan 2002; Meekan et al. 2003), as well as in the post-settlement stage (Searcy and Sponaugle 2001; Vigliola and Meekan 2002; McCormick and Hoey 2004).

In larval fishes, the process of growth reflects the interaction of an individual's developmental physiology with a great range of physical and biological factors. These may act either directly or indirectly to influence growth rates. For example, water temperature may determine developmental time, growth, swimming performance (Meekan et al. 2003; Green and Fisher 2004) and the rate of yolk sac absorption (Fukahara 1990) of young fish. Additionally, some species exhibit an optimal temperature range for development, outside of which mortality and abnormalities increase (Polo et al. 1991). Physical factors may also interact with other biological processes to influence growth rates. Wind speed and direction determine small-scale turbulence in the water column and may therefore indirectly be an important influence on rates at which larval fish encounter and capture prey (Gallego et al. 1996; Dower et al. 1997; Utne-Palm and Stiansen 2002). Similarly, as fish larvae are visual predators, factors such as the amount of solar radiation may either aid feeding by increasing the visibility of prey, or reduce survival by rendering fish more visible to other predators (Fortier et al. 1996). Solar radiation may also reduce larval survival through the damaging effect of ultraviolet radiation on nucleic acids or through epidermal damage (Zagarese and Williamson 2001), or indirectly through its impact on secondary production (Kouwenberg et al. 1999).

The aim of this study was to determine the influence of water temperature, wind speed and direction, rainfall and solar radiation on planktonic growth, pelagic duration and settlement intensity of the Caribbean surgeonfish, *Acanthurus chirurgus*. The results provide new foci for future studies on processes affecting the growth and survivorship of pelagic larvae in tropical marine systems.

Materials and methods

Sampling

From January 1984 to January 1988, newly settled *Acanthurus chirurgus* were collected daily from two small patch reefs in Punta de San Blas, on the Caribbean coast of Panama (9°34′N, 78°58′W). These reefs were located about 2.5 km apart, in shallow water and were surrounded by beds of seagrass on the back-reef of a larger fringing reef. To reduce any potential for migration of newly settled individuals reef A (about 1 m deep) was about 25 m from any other reef, while reef B (about 1.5 m deep) was about 15 m from other areas of coral. *A. chirurgus* are strongly site-attached for the first few weeks after settlement. Newly settled *A. chirurgus* were collected using a hand net with the help of the anaesthetic Quinaldine. Further details and a map are in Robertson (1992). In the laboratory, total and standard lengths were recorded and the sagittal otoliths removed for processing.

Otolith analysis

Robertson (1992) showed that peaks in settlement of *Acanthurus chirurgus* occurred during the new-moon half of the lunar cycle. As relatively few fish settled each day, individuals collected from the patch reefs were pooled into lunar cohorts from full moon to full moon to increase sample sizes. Otoliths from a subsample of 30% of the settlers in a lunar cohort, or at least 15 fish, were analysed from each month. In 24 of 43 lunar months less than 15 individuals settled and therefore the otoliths of all individuals were processed. Within each month, catches were divided among 1-mm standard length (SL) size classes and a sub-sample removed in proportion to the abundance of fish in each size class.

Sagittal otoliths were mounted on a glass slide using thermoplastic cement (Crystalbond) so that the distal end of the otolith protruded over the edge of the slide. The otolith was then ground to the nucleus using wet lapping film (12–0.3 μm). The Crystalbond was reheated and the polished side of the sagitta was mounted face down on the slide, so that the rostral end of the otolith could be ground down to produce a thin transverse section incorporating the nucleus. Sections were viewed at 1,100× magnification using a compound microscope linked to a video camera and computer. The width of each successive increment in otoliths was measured as the distance between two consecutive opaque zones using an image analysis system (OPTIMAS). Increments were always analysed along the longest radius of the otolith. It was assumed that the first increment closest to the core was formed at the time of hatching (Thresher et al. 1989; Wellington and Victor 1989). Sagittal otoliths from 11 individuals were analysed three times to determine the error involved in counts and measurements of increments. Four fish with settlement marks (Wilson and McCormick 1999) on their otoliths were excluded from the analysis to avoid the confounding effects of immigration of settled fish to patch reefs on our estimates of settlement intensity. Due to the difficulties in identifying the details of microstructure at the otolith margin (Wilson and McCormick 1999) settlement marks are discernible only a few days after settlement.

A strong linear relationship between sagittal radius and standard length of newly settled *Acanthurus chirurgus* together with 25 post-settlement individuals

$(r^2 = 0.85,\ P < 0.001,\ n = 625)$ supported the assumption that there was a proportional relationship between otolith and somatic growth of young *A. chirurgus*. Daily deposition of increments within the otoliths of young *A. chirurgus* was validated as follows. Ten *A. chirurgus* were collected from patch reefs in Punta de San Blas using hand nets and the anaesthetic clove oil. These patch reefs were not the same reefs where daily samples of fish were collected. The fish were immediately transferred to an aquarium and allowed to acclimatise for several days. Of the 10 individuals, 8 survived this period and were then placed in an aquarium that contained a solution of 500 mg/l tetracycline in seawater. The aquarium was left in complete darkness for 24 h to allow the tetracycline to be incorporated into the otoliths of the fish. The fish were then removed and left in another aquarium containing clean aerated seawater for 16 days. At this time, fish were sacrificed and one sagittal otolith from each individual was processed for analysis as described above. The sagittal section was viewed under a high power microscope equipped with a UV light source. The number of increments following the fluorescent tetracycline mark within the otolith was counted and compared to the number of days fish were kept in aquarium after being marked. The sagittal otolith of six out of eight individuals displayed a fluorescent mark. Counts of increments from this mark to the edge of the otolith closely approximated the number of days the fish were left in an aquarium after their removal from the tetracycline solution (mean $= 16.7 \pm 0.3$ days; range $= 14$–18 days), confirming daily increment formation.

Environmental variables

As environmental monitoring in the Punta de San Blas began only in the early 1990s, the physical data used in this study were obtained from the Galeta Marine Laboratory on Galeta Point, approximately 5 km east of the entrance to the Panama Canal and 100 km northwest of Punta de San Blas. A previous study has shown that wind measured at Punta de San Blas is strongly correlated to wind strength and direction at Galeta Point (Robertson et al. 1999).

Hourly measurements of sea surface temperature, rainfall, wind speed and direction and solar radiation were available from monitoring at Galeta Point (see http://striweb.si.edu/esp/physical_monitoring/download_galeta.htm). Daily averages were calculated except for rainfall. This was recorded as a total (mm/day). Wind directions were separated into orthogonal components using cosine and sine functions that were then multiplied by the average daily wind speed to derive north–south (cosine) and east–west (sine) vectors. On a large spatial scale (10 s of km), the north–south component of the wind resulted in offshore-onshore winds, while the east-westerly component generated along-shore winds at our study sites.

Growth, settlement and pelagic larval duration (PLD)

The ages derived from otolith analyses were used as estimates of pelagic larval duration (PLD) since fish were collected on the day of settlement. Otolith growth was used as an estimate of somatic growth thus avoiding the errors introduced by back-calculation of fish size from otoliths (Chambers and Miller 1995). Otolith growth was measured over three time periods: from 0 to 6 days, 7 to 25 days and from 26 to 50 days after hatching. The first of these periods represents the likely duration of feeding by newly hatched larvae on food supplied by the yolk sac (Randall 1961). Bergenius et al. (2002) identified 7–25 days after hatching as a period of rapid growth of *Acanthurus chirurgus* that has a major influence on the magnitude of settlement and recruitment of this species. On average, the mean larval duration of *A. chirurgus* is 55 days; 50 days after hatching 92% of the individuals are still pelagic (Bergenius 1998). The final growth period thus encompassed most of the remainder of the PLD of this species.

As individuals collected during the same lunar month varied in the length of their PLD, monthly data sets of fish settlement were reorganised by the date on which individual fish had hatched before the relationship between environmental variables and larval growth was examined. Hatch-dates could easily be determined as otolith examination provided an estimate of age and the collection date of each individual was known. By reorganising monthly data sets of fish settlement by hatch-date, individual growth histories were standardised so that they could be compared with the environmental conditions experienced by individuals on each day of their larval lives. Growth, PLD and settlement data in lunar months with less than two newly settled individuals, after reorganising by hatch-date, were pooled with data of the succeeding month. From this information, a mean environmental history and averages of PLD and growth rates could be calculated for each individual fish and subsequently for each lunar cohort to reduce the variable nature of individual responses to environmental signals (Chambers and Leggett 1987). This yielded a data set of 36 lunar cohorts for which there was sufficient data to analyze (12 lunar months in the dry season and 24 lunar months in the wet).

Environmental variables were also compared with the magnitude of settlement on a monthly basis after settlement data sets had been reorganised by hatch-date. Catches were standardised to numbers per 100 m^2 and were log$_{10}$ transformed in order to reduce the effects of small-scale (10s to 100s of meters) patchiness in settlement (Doherty and Williams 1988).

Comparison of environmental and biological variables

The influence of the environmental variables on PLD, planktonic growth and settlement intensity was examined using multiple regressions. These were used to find

leading indicators for any time series (e.g. growth) from other time series without lagged effects (Davies 2002). Analyses were run three times. The first included only data sets from dry seasons, the second only data from wet seasons and the third analysis the complete data set. Multiple regression analyses were run using SAS (1987) software. The "all possible subsets technique" was used to produce an optimum predictive model. For q independent variables there are 2^q possible models to predict Y. Out of all possible models the best three for each q were selected based on maximum R^2 (the coefficient of multiple determination) and Mallow's Cp selection statistics. Mallow's Cp measures the best possible fit of a model based on whether or not the error mean square contains only random variation (Draper and Smith 1981). The best model was then selected based on the lowest Cp. As strong correlations among independent variables can mask or exaggerate outcomes of regression models, correlation matrices, partial correlations and tolerance levels were calculated for environmental variables and examined for evidence of collinearity. When strong collinearity was detected the environmental variable displaying the strongest correlation to other independent variables was excluded from the multiple regression. In all models, the adjusted coefficient of multiple determination (R^2_{adj}) was calculated and used for interpretation rather than the R^2, since the former takes into consideration the number of degrees of freedom (Quinn and Keough 2002). Environmental variables were often $\log_{10}$ transformed to conform to the assumption of normality made by the analysis. Bivariate and partial correlations were calculated using the SPSS statistical package.

As the outcomes of multiple regression analyses are very susceptible to outliers, Cook's distances (Cook's D) were calculated for each data point. This statistic estimated the amount residuals would change by excluding a case from computation in a regression analysis. Cases with a large Cook's D (i.e. extreme outliers) were removed from the analysis, as these can falsify parameter estimates of a regression model (Barnett and Lewis 1994).

Results

Environmental seasonality

There are two distinct seasons in Caribbean Panama, a wet season from mid-April to mid-December and a dry season for the remainder of the year (Cubit et al. 1989). Seasonal averages, maxima and minima of water temperature, rainfall, solar radiation, and wind speed recorded at Galeta Point for the period of the study are presented in Table 1. During the wet season from mid-April to mid-December winds are light and variable in direction (Fig. 1) and there are heavy rains. Strong on-shore winds from a northerly direction (Fig. 1), increased solar radiation and cooler water temperatures characte-

Table 1 Means, maxima and minima of environmental variables during wet and dry seasons measured at Galeta Point from July 1984 to December 1987. The data were recorded by the Marine Environmental Science Program of the Smithsonian Tropical Research Institute

Variable	Season	Mean ± SE	Maxima	Mininima
Temperature	Wet	28.18 ± 0.02	30.00	25.75
(°C)	Dry	27.06 ± 0.04	28.60	25.17
Rainfall	Wet	10.57 ± 0.68	204.60	0
(mm day^{-1})	Dry	1.35 ± 0.28	54.70	0
Solar radiation	Wet	3918.98 ± 55.91	7234.00	205
(watts m^2)	Dry	5183.54 ± 81.18	7291.00	819
Wind speed	Wet	2.55 ± 0.13	3.82	1.77
(ms^{-1})	Dry	5.37 ± 0.20	6.70	4.32

rise the dry season, which encompasses the remainder of the year.

Patterns of fish settlement

Settlement varied from 0 to 660 *A. chirugus* per 100 m^2 of patch reef per lunar month over the 43-month sampling period (Fig. 2). Settlement peaked from November through to January of each year. Settlement of *A. chirugus* on patch reefs was correlated ($r = 0.75$) to recruitment measured on eight large (>300 m^2) reefs spread over a 15 km^2 area that were censused during the week before the new moon, when settlement peaks (Robertson 1992), indicating that patch reef collections were a good estimate of larger scale patterns of recruitment.

Environmental correlates of larval growth

Otolith growth from 0 to 6 days after hatching When the data sets were pooled among seasons, rainfall and solar radiation had a weak influence on the growth of *Acanthurus chirurgus* during the first 6 days of planktonic life (Table 2). However, when dry and wet seasons were analysed separately, regression models accounted for greater amounts of variability in otolith growth in early larval life. In the dry season, solar radiation accounted for 57% of the variation in growth and these variables were negatively correlated (Table 2; R_p: -0.85; Fig. 3a). During the wet season, the model accounted for less (38%) of the variation in the data set, and rainfall and along-shore winds were selected by the model as factors that influenced early growth rates. The partial correlation between rainfall and early larval growth was negative (Table 2; R_p: -0.47), while the relationship between along-shore winds and growth was positive (Table 2; R_p: 0.53). During the wet season along-shore winds were dominated by winds from a westerly direction (Fig. 2).

Otolith growth from 7 to 25 days after hatching The regression model of the complete data set accounted for 38% of the variability in growth of *Acanthurus chirurgus*

Fig. 1 Average monthly along-shore wind (ms^{-1} × direction) and onshore-offshore wind (ms^{-1} × direction) at Galeta Point during the study period. *d* Represents months in the dry season and *w* indicates months in the wet season
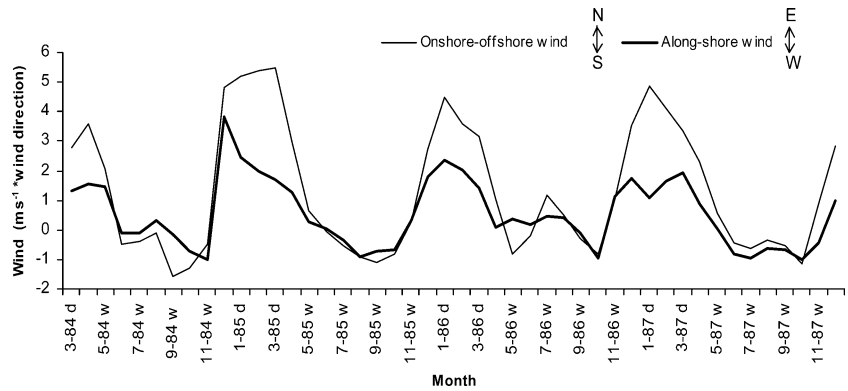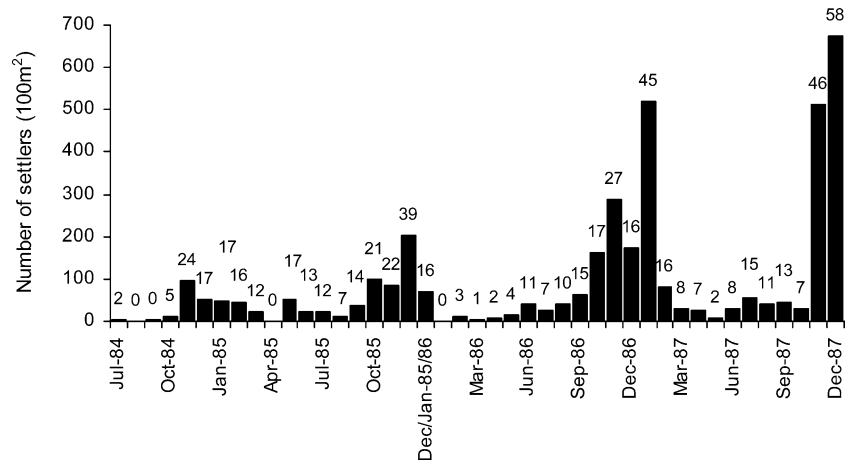

Fig. 2 *Acanthurus chirurgus.* Numbers of *A. chirurgus* settling per lunar month on two patch-reefs in Punta de San Blas in Panama, Caribbean, from July 1984 to December 1987. Settlers were standardised to numbers per 100 m². The *value above each bar* is the number of fish sampled for otolith analysis

between 7 and 25 days after hatching and identified only solar radiation as a significant influence on growth rates (Table 2; R_p: −0.58). In the dry season, along-shore winds and growth were highly correlated (Table 2; R: −0.94; Fig. 3b) and the regression model accounted for as much as 87% of the variation in growth. While the along-shore wind component was positively correlated with growth from 0 to 6 days, it was strongly negatively correlated with growth from 7 to 25 days after hatching. No significant relationship was found between the environmental variables and growth from 7 to 25 days after hatching during the wet season.

Otolith growth from 26 to 50 days after hatching Multiple regression analysis of the entire data set could not identify any combination of environmental variables that were correlated with growth between 26 and 50 days after hatching (Table 2). However, these analyses were significant when the data were split into wet and dry seasons. In the latter season, there was a strong positive correlation between rainfall and otolith growth (Table 2; R_p: 0.87; Fig. 3c). Growth at this time was also correlated with along-shore winds (Table 2, R_p: 0.66) and together these environmental variables accounted for 74% of the variation in growth. During the wet season, only 27% of the variability in larval growth could be accounted for by environmental factors (Table 2; rainfall and temperature; R_p: 0.55 and −0.49, respectively).

Environmental correlates of planktonic larval duration

As much as 65% of the variability in pelagic larval duration could be explained by a regression model that included solar radiation and along-shore winds (Table 2; R_p solar radiation: 0.64; R_p along-shore wind: 0.26). When regressions analysed wet and dry season data sets separately, along-shore winds accounted for 67% of the variability in PLD during the dry season (Table 2; R: 0.84; Fig. 4a), while solar radiation accounted for 23% of the variation in larval duration in the wet season (Table 2; R: 0.51).

Environmental correlates of settlement magnitude

Environmental variables accounted for only 22% of the variation in numbers of settlers arriving on patch reefs for the dry and wet seasons combined (Table 2). In this model, the magnitude of settlement was negatively correlated to solar radiation and water temperature (Table 2; R_p: −0.52 and −0.32, respectively). Analysis of dry season data produced a model that accounted for a greater amount of the variation in settlement (40%) and included the environmental variables of rainfall and solar radiation. Both were negatively correlated with settlement patterns (Table 2; R_p rainfall: −0.63 and R_p solar radiation: −0.70; Fig. 4b). Due to the high col-

Table 2 *Acanthurus chirurgus*. Summary of results of multiple regression analyses that compared water temperature (°C), rainfall (mm day^{-1}), solar radiation (watts m^{-2}), onshore-offshore wind (ms^{-1} × wind direction) and alongshore wind (ms^{-1} × wind direction) with larval growth (otolith growth in microns), pelagic larval duration (days) and settlement intensity of *A. chirurgus*. Larval growth was analysed from 0 to 6, 7 to 25 and 26 to 50 days after hatching. Analyses were repeated on the entire data set and on data separated into wet and dry seasons. See text for details of analysis techniques. $C(p)$ = Mallow's Cp (selection criteria), n = number of replicates (lunar months) included in the regression analysis, R^2 = coefficient of multiple determination, R^2_{adj} = adjusted coefficient of multiple determination, P (F-test) = significance values of the F-test associated with the ANOVA computed to test the null hypothesis: all the β's are 0 (β_i = pop- ulation parameter for the slope of the linear relationship between a dependent variable and an independent variables), where alpha was put at 0.05, *independent variables* = the environmental variables included in the optimum predictive model selected by the regression analysis, P (t-test) = significance values of the t-test computed to test the null hypothesis: β_i = 0, of the linear relationship between a dependent variable and an independent variables with all the other independent variables partialled out (i.e. it is a test for the partial correlations), ns = the F or t-test was not significant and in which the case significance value was not reported, R_p = partial correlation coefficient. The symbol ° = when only one variable was selected by the analysis Pearson's correlation coefficient (R) is given. The number of months identified as outliers and excluded from the analysis is in *parentheses* following the number of replicates

Dependent variable	Cp	R^2_{adj}	R^2	P (F-test)	Independent variables	R_p	P (t-test)
Growth 0–6 $n=35$ (1)	2.14	0.13	0.18	0.040	Rainfall	−0.42	0.014
					Solar radiation	−0.33	0.049
Growth 0–6 dry season $n=11$ (2)	4.94	0.57	0.73	0.038	Solar radiation	−0.85	0.004
					Onshore-offshore wind	−0.58	ns
					Along-shore wind	0.60	ns
					Rainfall	−0.54	ns
Growth 0–6 wet season $n=23$ (1)	2.77	0.38	0.47	0.007	Rainfall	−0.47	0.033
					Solar radiation	−0.35	ns
					Along-shore wind	0.53	0.013
Growth 7–25 $n=35$ (1)	1.93	0.38	0.41	0.000	Solar radiation	−0.58	<0.001
					Along-shore wind	−0.30	ns
Growth 7–25 dry season $n=10$ (2)	−0.5	0.86	0.88	0.000	Alongshore wind	−0.94 °	<0.001
Growth 7–25 wet season $n=24$	−0.04	0.01	0.04	ns	Solar radiation	−0.19 °	ns
Growth 26–50 $n=35$ (1)	4.94	0.15	0.22	ns	Temperature	−0.29	ns
					Rainfall	0.39	0.026
					Solar radiation	0.32	ns
					Along-shore wind	−0.23	ns
Growth 26–50 dry season $n=12$	1.84	0.74	0.79	0.001	Rainfall	0.87	<0.001
					Along-shore wind	0.66	0.026
Growth 26–50 wet season $n=23$ (1)	1.27	0.27	0.33	0.017	Temperature	−0.49	0.020
					Rainfall	0.55	0.008
PLD $n=35$ (1)	0.33	0.65	0.67	0.000	Solar radiation	0.64	0.000
					Along-shore wind	0.26	0.016
PLD dry season $n=12$	-0.75	0.67	0.69	0.001	Along-shore wind	0.84 °	0.001
PLD wet season $n=23$ (1)	0.89	0.23	0.26	0.013	Solar radiation	0.51 °	0.013
Settlers $n=36$	2.02	0.22	0.27	0.006	Solar radiation	−0.52	0.001
					Temperature	−0.32	0.045
Settlers dry season $n=12$	1.85	0.40	0.51	0.041	Rainfall	−0.63	0.037
					Solar radiation	−0.70	0.017
Settlers wet season $n=24$	2.20	0.13	0.21	ns	Rainfall	0.33	ns
					Onshore-offshore wind	0.42	0.045

linearity (R: 0.9) among wind variables and temperature in the dry season, the latter was excluded from the analysis. Multiple regression analysis could not identify a model that accounted for a significant amount of variation in settlement magnitude during the wet season.

Discussion

The strength and direction of the relationships between growth and environmental variables differed with larval stage, suggesting that the impact of the environment on growth of larval *Acanthurus chirurgus* is dependent on ontogeny. Moreover, correlations between planktonic growth, PLD, settlement intensity and environmental variables were stronger during the dry than the wet seasons and usually involved different combinations of environmental variables each season. This suggests that future studies of tropical fish larvae that examine the influence of environmental variables on early life history characteristics require the data to be analysed separately for each season, as is the case for temperate studies.

Growth

Different combinations of the environmental variables solar radiation, rainfall and along-shore winds accounted for a varying amount (from 13% to 86%) of the changes in otolith growth of *Acanthurus chirurgus* from hatching until the time of settlement. In the first 6 days

Fig. 3a–c *Acanthurus chirurgus*. **a** Partial regression plot of growth (microns) of *A. chirurgus* from 0 to 6 days after hatching and solar radiation (watts m²) during the dry season, corrected for the effects of along-shore wind (ms⁻¹ × wind direction), onshore-offshore wind (m/s × wind direction) and rainfall (mm/day). **b** Regression plot of growth (microns) from 7 to 25 days after hatching and along-shore winds (ms⁻¹ × wind direction) during the dry season. **c** Partial regression plot of growth (microns) from 26 to 50 days after hatching and rainfall (mm/day) during the dry season, corrected for the effect of along-shore wind
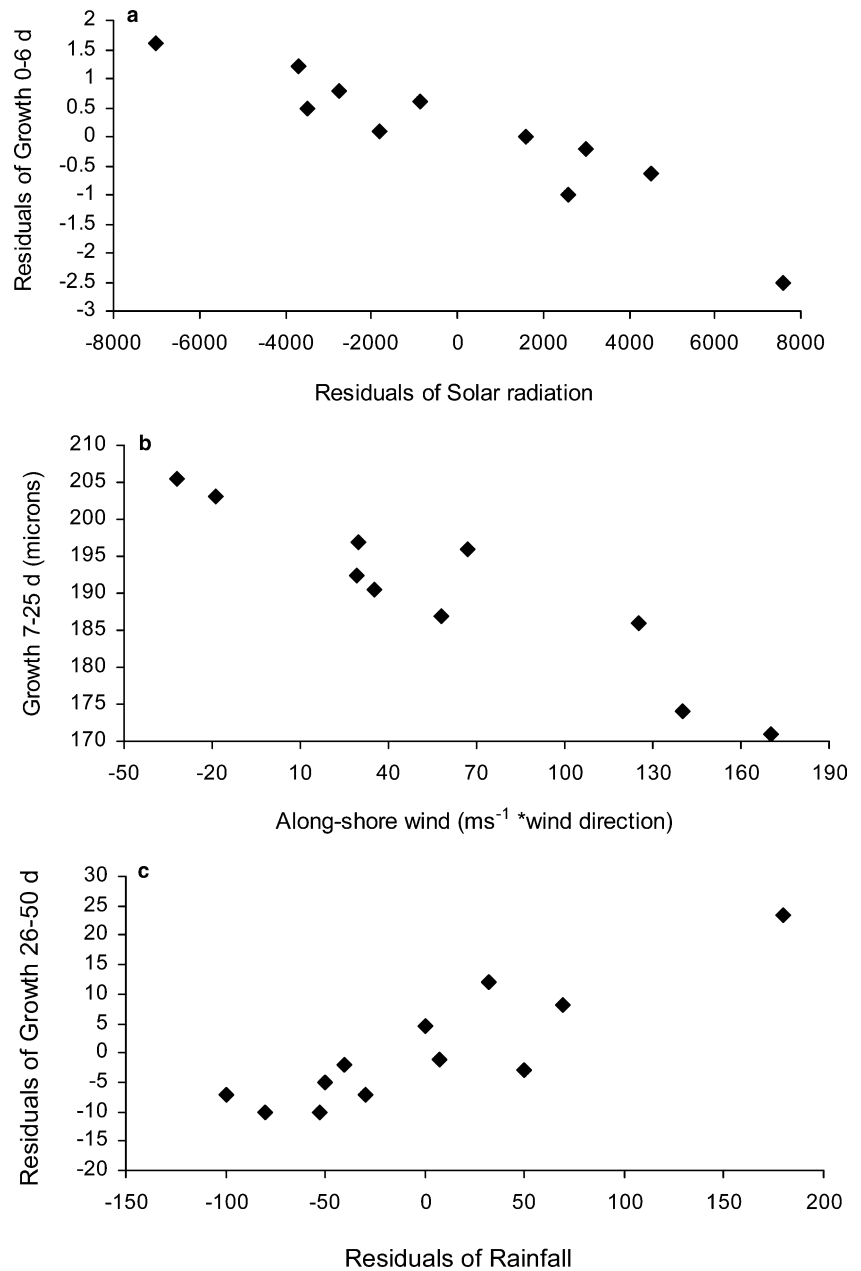
of larval life, growth rates were negatively correlated with the amount of sunlight during the dry season, a result that contrasts with the outcomes of previous studies. Typically, these have found that sunlight has a positive, albeit indirect effect on larval growth (Heath et al. 1988; Gallego et al. 1996) by warming surface waters and increasing food production (Cushing 1990; Heath 1992; 1995). Recent work, however, has shown that high levels of light may negatively affect fish larvae. Ultraviolet radiation may induce direct damage to the DNA and proteins of eggs and larvae, causing reduced growth or death (Lesser et al. 2001; Zagarese and Williamson 2001). Moreover, Boeuf and Le Bail (1999) suggest that beyond an upper intensity, sunlight may decrease growth and even be deadly due to negative impacts on visual development, which in turn will affect feeding activities and prey selection. Our results suggest that the high levels of sunlight that occur during the dry season in Punta de San Blas may detrimentally affect growth rates. Alternatively, sunlight may make larvae more susceptible to predators during early developmental stages, when sensory and locomotory systems are poorly developed. This may affect survivorship or could force young fish deeper in the water column, away from the depth of optimal light intensities for feeding and growth (Fortier and Harris 1989).

In addition to sunlight, rainfall was also negatively correlated with growth of *Acanthurus chirugus* up to 6 days after hatching, although unlike solar radiation, this correlation was significant during the wet season.

Fig. 4a, b *Acanthurus chirurgus*. **a** The regression relationship between pelagic larval duration (PLD; days) and along-shore winds (ms^{-1} × wind direction) during the dry season. **b** Partial regression plot of number of settlers and solar radiation (watts m^2) during the dry season, corrected for the effect of rainfall (mm/day)
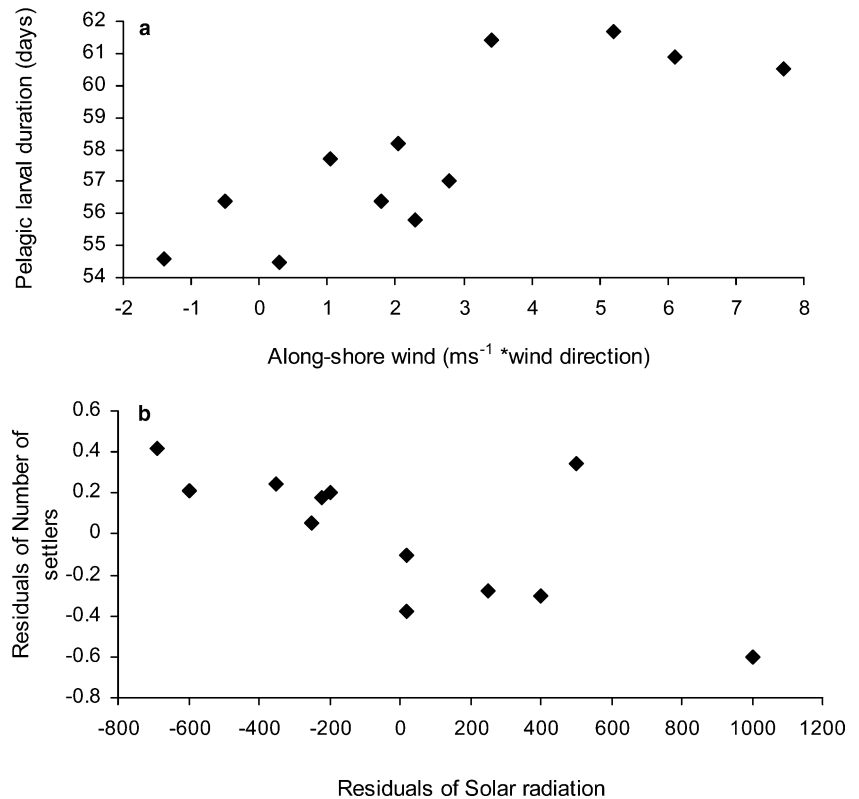
Heavy rains in the wet season that decrease salinity in surface layers may be detrimental to young larvae due to their small surface to volume ratio and lack of protective scaling against changes in the osmotic environment. A turbid upper layer of fresh water may also reduce light penetration and thus feeding by young fish. However, heavy rains are also associated with increased run-off from rivers and nutrients in inshore environments (D'Croz et al. 1999), potentially resulting in better feeding conditions for larger, more developed larvae. This may explain the positive relationship between rainfall and growth of larvae 26–50 days after hatching in both the dry and the wet seasons.

There was a complex relationship between growth of *Acanthurus chirurgus* larvae and winds. Growth up to 6 days after hatching was positively correlated with along-shore winds, negatively correlated from 7 to 25 days after hatching and again positively correlated with along-shore winds after 25 days. While variations in winds might influence growth at local scales by directing the surface waters and the food sources they contain away from or along the coast, little evidence exists to assess this possibility. It has been hypothesised that winds may affect growth in larval fish due to their influence on small-scale turbulence. At optimum levels, turbulence is thought to increase the probability of encounter between larval fish predators and their prey, thus increasing growth rates and survivorship (Gallego et al. 1996; Dower et al. 1997). It is possible that the complex relationship between growth and wind identified in this study is actually a reflection of a change in the

interaction between wind-induced turbulence and growth throughout ontogeny.

Water temperature was not significantly correlated with growth rates of larval *Acanthurus chirugus* in the first 25 days of larval life, although there was a weak negative correlation between these variables after this time during the wet season. This result differs from studies in temperate and other tropical regions where water temperature is thought to be one of the primary determinants of growth rates (Campana and Hurley 1989; Suthers and Sundby 1993; Meekan et al. 2003). In tropical NW Australia, Meekan et al. (2003) found that water temperature explained 30% of the variation in growth rate of a larval pomacentrid. These contrasting results may be due to the relatively small temporal (seasonal, monthly and diurnal) ranges in temperatures that occur in Punta de San Blas (Table 1).

Pelagic larval duration

Our analysis suggested up to 65% of the variability in the PLD of *Acanthurus chirugus* could be accounted for by a regression model that included the variables of along-shore winds and solar radiation. When seasons were analysed separately, along-shore winds were strongly correlated with PLD in the dry season ($R = 0.84$), while solar radiation was moderately correlated ($R = 0.51$) with PLD in the wet season. The positive relationship between along-shore winds and PLD is surprising, given that such winds were positively corre-

lated to early and late larval growth. Fast growing larvae might be expected to have shorter larval durations than slow growing larvae and we found a significant negative correlation between average growth to settlement and larval duration (regression analysis, $r^2 = -0.45$ $P < 0.001$, $n = 603$). One possibility that might account for this result is that some compensatory growth occurred during the late larval phase, so that larvae that were small at earlier stages grew relatively fast at this time. Such explanations assume that larvae do not typically delay settlement, and this delay appears to be the case in this species (Bergenius 1998).

Our results suggest that solar radiation (and with it UV radiation exposure) may have a negative effect on the development of the pelagic eggs and larvae of acanthurids, as there was a positive correlation between solar radiation and PLD of *Acanthurus chirurgus* during the dry season. Recent work suggests that the early life history stages of fishes and invertebrates are particularly sensitive to the UV radiation present in natural sunlight (Lesser et al. 2001; Zagarese and Williamson 2001). The positive correlation between solar radiation and PLD was consistent with the negative relationship between solar radiation and otolith growth up to 25 days, since a longer larval duration is likely to be a consequence of decreased growth.

Numbers of settlers per lunar month

Solar radiation and temperature explained 22% of the variability in numbers of settlers arriving on patch reefs each lunar month when data were pooled between seasons. When analysed separately, solar radiation and rainfall were both negatively correlated with settlement and the regression model described 40% of the variability in settlement intensity. The effect of these variables on settlement might be explained by their influence on growth rates, given that Bergenius et al. (2002) and Wilson and Meekan (2002) have demonstrated that growth during the early larval stages is an important determinant of the numbers of fish surviving the planktonic phase. As noted previously, high levels of sunlight may decrease growth rates or increase egg mortality rates (Frank and Leggett 1981). Similarly, if heavy rains, which also occur occasionally in the Caribbean during the dry season, dramatically change osmotic environments, there might be a resulting increase in mortality of fish eggs and newly hatched larvae.

Our study suggests that the environmental variables of solar radiation, along-shore winds and rainfall may be used to predict the growth of *Acanthurus chirurgus* larvae at different stages of their pelagic life and that the impact of environmental variables on replenishment may vary between seasons. To date, most studies of the effects of the environment on life history characteristics of marine fishes have examined only one environmental variable. We suggest that the outcomes of such studies should be treated with caution and that as many vari-

ables as possible should be included in tests of environmental influences.

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